Benthic Invertebrate Fauna, Small Streams

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Introduction

Small streams (first- through third-order streams) make up >98% of the total number of stream segments and >86% of stream length in many drainage networks. Small streams occur over a wide array of climates, geology, and biomes, which influence temperature, hydrologic regimes, water chemistry, light, substrate, stream permanence, a basin's terrestrial plant cover, and food base of a given stream. Small streams are generally most abundant in the upper reaches of a basin, but they can also be found throughout the basin and may enter directly into larger rivers. They have maximum interface with the terrestrial environment, and in most temperate and tropical climates they may receive large inputs of terrestrial, or allochthonous, organic matter (e.g., leaves, wood) from the surrounding plant communities. In locations with open canopies such as grasslands and deserts, autochthonous or primary production in the form of algae, or higher aquatic plants, may serve as the main food base. Hence, headwater streams display a diverse fauna, which is often adapted to physical, chemical, and biotic conditions of the region.

Diversity of Benthic Invertebrates in Small Streams

The benthic invertebrate fauna of small streams is composed primarily of aquatic insects, crustaceans, mollusks, and various other invertebrate taxa. The insect fauna consists primarily of Odonata (dragonflies and damselflies), Ephemeroptera (mayflies), Plecoptera (stoneflies), Megaloptera (alderflies and dobsonflies), Coleoptera (beetles), Trichoptera (caddisflies), occasional Lepidoptera (moths), and Diptera (true flies). Crustaceans (including amphipods, isopods, and crayfish) can also be found in small streams as well as microcrustaceans such as cladocerans, ostracods, and copepods. Other common invertebrates found in small streams include nematodes, oligochaetes, turbellarians, and mollusks such as snails, limpets, and finger-nail clams. Total invertebrate diversity in small streams can be quite high. The Breitenbach, a first-order stream in Germany, contains at least 1004 described invertebrate taxa. At least 293 invertebrate taxa have been found in headwater streams in the southern Appalachian mountains of the United States. Over 182 known invertebrate taxa have been recorded in a mountain stream on Bougainville Island, Papua New Guinea. Incredibly, there are many headwater invertebrate species that remain undescribed in both isolated and populated regions of the world.

With the great diversity of foods available for consumption by invertebrates (i.e., deposited and retained on substrates, or suspended in the water column), it is not surprising that invertebrates have evolved diverse morphobehavioral mechanisms for exploiting food resources. Their diverse feeding behaviors have been lumped into a broad functional classification scheme, which is based on mechanisms used by invertebrates to acquire foods. These functional groups are as follows: scrapers, animals adapted to graze or scrape materials (periphyton, or attached algae, fine particulate organic matter, and its associated microbiota) from mineral and organic substrates; shredders, organisms that comminute large pieces of decomposing vascular plant tissue such as leaf detritus (>1 mm diameter) along with its associated microflora and fauna, or feed directly on living vascular hydrophytes, or gouge decomposing wood; gatherers, animals that feed primarily on deposited fine particulate organic matter (FPOM $\leq$ 1 mm diameter); filterers, animals that have specialized anatomical structures (e.g., setae, mouth brushes, or fans) or silk and silk-like secretions that act as sieves to remove particulate matter from suspension; and predators, those organisms that feed primarily on animal tissue by either engulfing their prey, or piercing prey and sucking body contents.

Functional feeding groups refer primarily to modes of feeding and not type of food per se. For example, many filter-feeding insects of high gradient streams are primarily carnivores, whereas scrapers consume quantities of what must be characterized as epilithon, a matrix of polysaccharide exudates, detritus, microflora, and microfauna associated with stone surfaces, and not solely attached algae. Shredders may select those leaves that have been 'microbially conditioned' by colonizing fungi and bacteria. Shredders also ingest attached algal cells, protozoans, and various other components of the fauna during feeding. Some 'shredders' have been shown to grow by harvesting primarily the epixylic biofilm, the matrix of exudates, detritus, microflora, and microfauna found on wood surfaces. Although it appears valid to separate benthic invertebrates according to these mechanisms used to obtain foods, many questions remain concerning

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the ultimate sources of protein, carbohydrates, fats, and assimilated energy to each of these functional groups.

Quantitative Measurements of Benthic Invertebrates in Headwater Streams

Invertebrates are often enumerated by abundances or average numbers per unit area of stream bottom. Other measures include average biomass, or weight, per unit area of stream, or more rarely, secondary production per unit area of stream bottom. Each of these will provide a different picture of the invertebrate community. For example, Figure 1(a) shows abundances per unit area of moss-covered bedrock outcrop and mixed substrates in three headwater streams ($n = 20$ total stream years) at the Coweeta Hydrologic Laboratory in western North Carolina, USA. Note that abundances are dominated by members of the collector-gatherer (Cg), functional group. In contrast, three groups, predators, shredders, and collectors, represent the majority of the biomass in these small streams (Figure 1(b)). Secondary production, which represents the living organic matter or biomass produced by each functional group over a year regardless of its fate, i.e., losses to predation, or other sources of mortality, is fairly evenly distributed between the predator, collector, and shredder functional groups (Figure 1(c)). The integration of production, feeding habits, and bioenergetic data can yield a much better understanding of the role of animal populations in ecosystem function than either abundance or biomass.

Distributional patterns for functional feeding group abundance, biomass, and production in small streams may differ among substrate types (Figure 1(a)–1(c)). Collectors and predators dominate abundances on both substrates. For biomass, predators > shredders > collectors dominate the mixed substrates, whereas filterers > collectors > predators contribute most to biomass on bedrock outcrop substrates. Most production is attributed to predators > shredders > collectors in mixed substrates compared to filterers > collectors > predators on bedrock out crop substrates. Thus, distinct differences exist in functional feeding group production among different substrates within a stream, which correspond to different available food resources. Filterer production predominates in the bedrock habitats with high current velocities that transport FPOM. Collector production is also enhanced by FPOM trapped in the moss on the bedrock outcrops. Conversely, predator, shredder, and collector production are similar in the retentive mixed substrate habitats, which also have the greatest biomass, abundances, and organic matter retention. Scraper abundance, biomass, and production are low for all

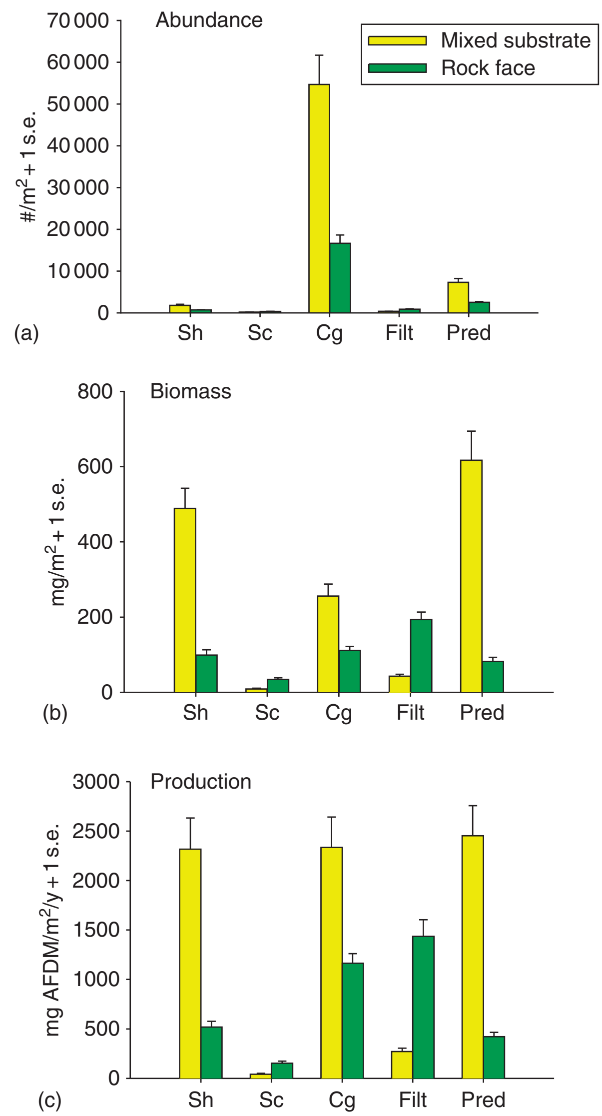

Figure 1 Total abundance, biomass, and production of invertebrates by functional feeding group for mixed substrate and rockface habitats in headwater streams at Coweeta Hydrologic Laboratory in western North Carolina, USA. These data represent 20 total years of abundance, biomass, and production estimates.

habitats as these small streams are heavily shaded year round by dense riparian rhododendron. These data emphasize the influence of local geomorphic processes and riparian linkages on invertebrate productivity in forested headwater streams.

Comparison of Secondary Productivity Measurements from Small Streams

Secondary productivity measures for benthic invertebrates from small streams from various temperate areas around the world are given in Table 1. Total annual productivity is quite variable ranging from

Table 1 Estimates of secondary production (g m^{-2} year^{-1}) for various functional feeding groups, or primary and secondary consumers, for small streams from various regions of the world

Country	*Biome*	*Stream*	*Scrapers*	*Shredders*	*Collectors*	*Filterers*	*Predators*	*Total production*	*Source*
USA, ID	Cool desert	Douglas Creek*	2.65	0.64	15.28	4.20	0.45	23.22	2
USA, ID	Cool desert	Snively Springs*	0.00	1.32	9.33	3.18	0.33	14.15	2
USA, ID	Cool desert	Rattlesnake Springs*	0.00	0.17	3.62	11.80	0.77	16.36	2
Denmark	Deciduous	Rold Kilde	0.14	5.93	2.58	0.01	0.88	9.54	6
USA, NC	Eastern deciduous	Coweeta Catchment 53	0.09	3.23	5.78	0.56	4.10	13.77	7
USA, NC	Eastern deciduous	Coweeta Catchment 54	0.22	3.53	3.77	0.72	3.17	11.41	7
USA, NC	Eastern deciduous	Coweeta (1985) Catchment 55	0.17	2.51	2.86	0.73	2.52	8.79	7
USA, NC	Eastern deciduous	Coweeta (1986) Catchment 55	0.50	2.75	3.41	0.54	3.37	10.57	7
USA, NC	Eastern deciduous	Upper Ball Ck	0.68	1.67	2.95	0.53	1.68	7.51	5
USA, NC	Eastern deciduous	Bear Pen Ck	0.68	2.02	4.45	2.32	1.66	11.12	12
USA, VA	Eastern deciduous	Buzzard's Branch	0.11	2.84	6.21	0.98	3.78	13.92	10
USA, VA	Eastern deciduous	Collier's Ck	0.11	1.69	0.95	1.28	1.58	5.60	10
USA, NH	Eastern deciduous	Bear Brook	0.74	1.45	0.61	0.43	0.94	4.17	3
USA, ME	Eastern deciduous	Goosefare Brook	0.16	11.78	5.28	3.96	5.20	27.35	13
USA, ME	Eastern deciduous	West Bear Brook	$<$0.00	0.86	0.21	0.22	0.37	1.66	1
USA, ME	Eastern deciduous	East Bear Brook	$<$0.00	0.80	0.20	0.27	0.41	1.68	1
USA, KS	Tall grass prairie	Kings Creek	3.80	4.50	6.00	1.70	3.60	19.60	11
Germany	Deciduous forest	Steina (1986)	4.63	5.10	4.53	2.43	2.33	19.02	8
Germany	Deciduous forest	Steina (1987)	7.96	2.38	3.84	3.72	2.93	20.83	8

Continued

Table 1 Continued

Country	*Biome*	*Stream*	*Scrapers*	*Shredders*	*Collectors*	*Filterers*	*Predators*	*Total production*	*Source*
The following studies calculated production based on primary and secondary consumers rather than functional groups									
			Total primary consumer production[a]			Total secondary consumers production[b]		Total production	
USA, MA	Eastern deciduous	Factory Brook*	4.00			0.56		4.56	9
New Zealand	Tussock Grass	Sutton Stream	13.35			2.54		15.89	4

Note that data for those streams marked with an asterisk were in dry mass (DM), whereas others were in ash-free dry mass (AFDM) DM values are ~10–20% greater than AFDM.

[a]Primary consumers includes scraper, shredder, collector, and filterer functional feeding groups.

[b]Secondary consumers = predators.

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<2 to >27 g m^{-2} year^{-1} for streams in a variety of landscapes (Figures 2–10). The following is an indication of the average secondary production (percentage of total) in invertebrates: collectors (31.2%, range 11.9–65.9%) > shredders (avg. = 27.0%, range 1–62.2%) > predators (avg. = 19.0%, range 1.9–31.9%) > filterers (avg. = 15.1%, range 0.1–72.1%) > scrapers (avg. = 7.4%, range = 0.0–38.2%). Scraper production as a percent of total production was greatest in the Steina, Germany (deciduous forest), followed by Kings Creek, a tall grass prairie stream in Kansas, and Bear Brook, NH (deciduous forest). The differences in scraper production in small streams in the eastern deciduous forest are striking. In Bear Brook NH, scraper production comprised >17% of total production, compared with 0.7–9% for the Coweeta streams in NC, which are heavily shaded by dense riparian rhododendron. With the exception of three cold desert streams in southeastern Washington, USA, shredder production was always greater than 10% of the total production. Percent collector–filterer production was lowest in a Danish Spring and highest in a cool desert stream. These data demonstrate that invertebrate production in small streams can be quite variable among various temperate regions. Given the usefulness of this integrative measure for comparing small stream functioning in natural and disturbed environments, additional efforts at quantifying total secondary production in small streams are badly needed.

Figure 2 A steep-gradient headwater stream in the Appalachians of western NC. Note the dense rhododendron understory, which shades the stream. (Photo by S. L. Eggert.)

Factors that Influence Invertebrates in Small Streams

Small stream invertebrates are influenced by physical, chemical, and biological factors (Table 2). Physical factors include climate, (e.g., temperature and

Figure 3 Headwater stream draining catchment 53 at the Coweeta Hydrologic Laboratory in western North Carolina during autumn. Note large amounts of leaves and woody debris in the stream channel. (Photo by S. L. Eggert.)

Figure 4 Headwater stream draining watershed 6 in the Hubbard Brook Experimental Forest in central New Hampshire, USA. (Photo by R. O. Hall.)

Figure 5 Intermittent stream in the Huron Mountains of Michigan's upper peninsula, USA. (Photo by S. L. Eggert.)

precipitation), hydrology, and geology. Hydrology and the frequency of flooding or drying can also influence community structure and productivity. For example, the lowest annual productivity shown in Table 1 occurs in two intermittent streams, East Bear Book and West Bear Brook in Maine, USA. Geology influences both stream substratum and chemistry. Substratum and the proportions of eroding and depositional substratum within a given stream can have an important effect on invertebrate functional distribution and production. The faster flowing erosional reaches in small streams are often dominated by filter-feeders and scrapers, whereas depositional reaches with greater amounts of retained organic matter are often dominated by shredders and collectors. Stream chemistries can be strikingly different from those in nearby streams if they have different underlying geologies. For example, in the southern Appalachians, streams draining limestone regions such as the ridge and valley province have higher nutrients, conductivity, pH, and primary production than those draining the crystalline Appalachians. Geology and climate also influence the vegetation of catchments, including the abundance and type of

Figure 6 Bison grazing in the riparian area of the headwaters of King's Creek, at the Konza Prairie LTER in Kansas, USA. (Photo by Walter Dodd.)

Figure 8 Rattlesnake Creek, a cold desert stream in eastern Washington, USA. (Photo by C. E. Cushing.)

Figure 7 Douglas Creek, a cold desert stream in eastern Washington, USA. (Photo by C. E. Cushing.)

riparian vegetation. Streams that are open, and which receive large solar inputs compared with those draining dense forested catchments, may have a very different food base (autochthonous) compared with those receiving primarily allochthonous inputs from forested catchments. Depending on the food base, small streams may display large differences in functional group abundance, biomass, and production.

Figure 9 A spring-fed tundra stream in Alaska, USA. (Photo by A. D. Huryn.)

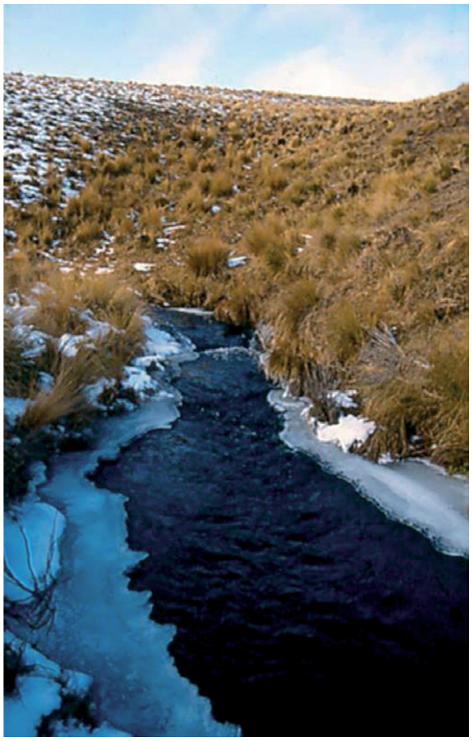

Figure 10 A stream draining tall tussock grass on South Island, New Zealand. (Photo by A. D. Huryn.)

Ecological Roles of Invertebrates in Small Streams

Feeding activities of invertebrates in small streams link headwater streams to larger rivers downstream by altering resource quantity, size, and shape (Table 2). For example, the shredding of leaf detritus and woody debris by shredders in headwater streams increases the rate of coarse organic matter breakdown to fine organic matter, which is transported by the current to downstream reaches. Scrapers, through their feeding activities and dislodging of epilithon, can enhance the movement of downstream organic particles. Heavy grazing by scrapers results in periphyton mats with adnate, or closely attached forms of diatoms that are less susceptible to scouring during disturbances such as large storms and also promotes nutrient turnover in periphyton communities. Thus, both shredding and grazing activities may result in a consistent, prolonged release of materials to downstream reaches, in contrast to large storms that induce pulsed massive export over short time intervals. The role of gatherers in FPOM transport has been implicated in an Idaho stream, which exhibited continuous deposition and resuspension as particles moved downstream. In montane Puerto Rican streams, feeding activities of atyid shrimp reduce organic matter accrual on benthic substrates. Other invertebrate gatherers such as *Ptychoptera* (Diptera: Ptychopteridae) and sericostomatid (Trichoptera) larvae may transfer fine organic matter buried in depositional areas to substratum surfaces as feces.

Filter-feeding stream invertebrates enhance retention of organic matter and nutrients. Certain invertebrates can transport superficial organic matter to deeper sediments, which reduces downstream transport. However, direct removal of transported material by filter-feeders has received the bulk of attention and has been shown to have variable effects on retention depending on size of stream, abundance of filterers, and taxon-specific differences in feeding, (e.g., feeding on extremely fine organic particles or drifting invertebrates). Studies using radioactive tracers in Alaskan streams have also suggested that particles generated by invertebrate scrapers such as baetid mayflies and chironomid larvae were instrumental in supplying fine particles to downstream black flies. Microfilterers such as the caddisfly family Philopotamidae, and black flies (Diptera: Simuliidae), and bivalve mollusks increase particle sizes by ingesting minute particles and egesting compacted fecal particles larger than those originally consumed. Such microfilterers perform two very important functions in streams. First, they remove FPOM from suspension (which would otherwise pass unused through the stream segment) and second, they defecate larger particles, which are available to deposit-feeding detritivores.

Predators can play numerous roles at scales ranging from individuals to ecosystems and invertebrate predators in small streams are no exception. Predators can influence export and retention of energy and nutrients through their effects on the standing stocks of other functional groups. Other mechanisms include decreasing rates of nutrient cycling by immobilizing nutrients in long-lived predator taxa versus short-lived prey. Besides direct consumption, foraging by invertebrate predators can enhance invertebrate drift and suspended FPOM, which also increases export of nutrients. Invertebrate predators can enhance retention of organic matter by retarding breakdown rates of leaf litter as well as subsequent generation of FPOM. Predaceous stoneflies and caddisflies can significantly decrease the rate of leaf litter processing by reducing shredder populations in leaf packs. Invertebrate predators can also increase the rate of downstream movement of organisms and sediment. Many stream invertebrates exhibit different responses to fish and invertebrate predators, and the local impact of invertebrate predation on benthic prey may exceed the impact of fish predators. In the presence of fish, invertebrate prey often reduces movement and seeks refuge in the substrate. In contrast, invertebrate

Table 2 Factors influencing benthic macroinvertebrates and effects of invertebrates on stream processes in headwater streams

Factor	*Effect on benthic macroinvertebrates and stream processes*	*Source*
Physical		
Water temperature	Lower water temperature resulted in higher total taxa richness and Ephemeroptera, Plecoptera and Trichoptera richness; snail production regulated by thermal regime; water temperature positively related to growth rates of invertebrates	5, 20, 21, 47
Hydrology	Functional feeding group production determined in part by hydrology; current velocity affected invertebrate movement and drift; channel drying altered organic matter standing crops, and invertebrate abundance and production; invertebrate abundance and diversity declined as a result of severe flow diversions	4, 19, 22, 35, 41
Geology	Higher alkalinity resulted in greater benthic invertebrate abundance, biomass, drift biomass, and organic matter standing crop; higher snail biomass and caddisfly production	20, 23, 24, 27
Substrate	Invertebrate taxa show distinct substrate preferences; functional feeding group production varied with factors associated with stream geomorphology; invertebrate diversity and abundance increases with substrate stability and presence of detritus	9, 22, 30
Chemical		
pH	Low pH resulted in decreased taxa richness, loss of sensitive taxa (Mollusca, Crustaceans, Ephemeroptera); increased drift immediately after acidification; decreased emergence; long-term decreased abundance and drift; reduced Ephemeroptera growth; reduced leaf breakdown rates; increased detritus standing crop	2, 11, 13, 16, 17, 39, 45
Conductivity	Loss or reduction of Ephemeroptera at conductivities $>400\ \mu S/cm$; reduced Ephemeroptera, Plecoptera, and Trichoptera diversity with increased conductivity; replacement of sensitive Ephemeropteran taxa with tolerant Dipteran taxa with increasing conductivity	14, 32, 38
Nutrients	Increase in abundance, biomass and production of invertebrates; increased growth rates for short-lived invertebrates; increased growth and abundance of limnephilid caddisflies in the presence of salmon carcasses	7, 8, 51
Biological		
Riparian vegetation	Invertebrate distribution, abundance, biomass, production, diversity, and growth rates, as well as leaf breakdown rates, were strongly related to riparian vegetation composition	1, 15, 29, 34, 42, 46, 52
Competition	Evidence of interspecific competition: between snail and caddisfly grazers, between caddisfly and mayfly grazers, between net-veined midges and blackflies, and between caddisflies and filterers; intra- and interspecific competition between snails; intraspecific competition for Trichopteran and Ephemeropteran shredders. Competition resulted in varied responses with regard to survivorship, growth rates, colonization of habitat, and feeding rates.	3, 6, 12, 18, 25, 26, 33
Predation	Predation on shredders resulted in reduced leaf breakdown and FPOM generation; predation on scrapers resulted in increase periphyton biomass; long-lived predators retain nitrogen; predation causes downstream movement of inorganic material; predators cause prey to drift or seek refuge in the substrate	26, 31, 37, 43, 44, 54

Continued

Table 2 Continued

Factor	*Effect on benthic macroinvertebrates and stream processes*	*Source*
Altered resource size and shape	Grazing caddisflies increase algal turnover; shredders convert large organic matter to FPOM; microfilterers increase particle size	28, 36, 55
Material transport	Gatherers feeding on and egesting FPOM enhance downstream transport; invertebrates transfer FPOM to surface as feces; shrimps reduce organic matter accrual on substrates through feeding	10, 40, 48, 53, 55
Material retention	Incorporation of labeled nitrogen by scrapers and filters downstream; microfilterers retain FPOM; filterers reduce downstream transport of particulate organic matter	37, 49, 50

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predators have the ability to search in sites similar to those being used by their prey, and the latter may respond by actively entering the water column and drifting downstream. Foraging by invertebrate predators can also influence the downstream movement of inorganic material through their physical activities. Several studies have suggested that the foraging activities increase erosion and downstream transport of sand and fine sediments. Furthermore, some specialized parasites (a subcategory of predators) of scraping *Glossosoma* caddisflies have been shown to influence periphyton biomass in Michigan streams.

Anthropogenic and Natural Disturbances to Invertebrate Productivity in Small Streams

Many unique fauna are found in small streams. Unfortunately, invertebrate fauna in these streams are under assault by anthropogenic and natural disturbances such as invasive species, agriculture, development, logging, mining, recreational activities, global climate change, and wildfires (Table 3). Macroinvertebrate communities and productivity can be altered, which can affect higher trophic levels (e.g., fish production) and other stream processes (e.g., organic matter processing).

Invasive Species

Invasive species within riparian habitats can have lasting effects on headwater stream functioning because of the tight linkage between riparian forests and stream processes. Macroinvertebrates abundance and diversity in small streams can be altered by changes in microclimate, energy availability, and habitat that results from loss of tree species within the riparian forest. Outbreaks of terrestrial invaders such as the balsam and hemlock woolly adelgids and the gypsy moth result in losses of some riparian tree species, pulses of slow decaying wood inputs, increases in other tree species, and increases of pesticides used to control invading pests. Indirectly, these changes can affect headwater stream functioning through reductions in the survival, growth, and emergence of macroinvertebrate shredders and detrital processing. The effects of terrestrial invasive species on stream ecosystems are expected to increase in the future. Nonnative scale and fungal diseases such as dogwood anthracnose and beech bark disease have invaded forests of the eastern United States, and the fungus causing butternut canker is beginning to spread rapidly. The fungus causing chestnut blight eliminated the American chestnut from eastern forests and resulted in decreased leaf litter processing, decreased quality of litter inputs, and decreased invertebrate growth rates in headwater streams. The input of dead chestnut logs into streams also facilitated the retention of sediment and served to stabilize stream channels. Few examples of exotic aquatic species invading small streams have been documented in the literature. One species that successfully invaded first- and second-order streams, *Gammarus pulex*, resulted in spatial and temporal reductions in macroinvertebrate diversity.

Agriculture

The filling of former wetlands and headwater streams for agriculture has greatly reduced surface water area worldwide. As an example, 96.6% of the original surface water area of the Kävlinge River catchment in Sweden has been lost due to channelization and drainage of streams for agriculture over a 141-year period. Along with the loss of small streams, intensive agriculture results in excessive nitrate levels in stream water. Overfertilization of agricultural land in low-order sections of river networks affects downstream river reaches. It has been estimated that agricultural sources in Illinois contribute 10–15% of nitrogen and phosphorus loads to the Mississippi River. Nutrient enrichment in small streams can stimulate primary production and higher trophic levels such as scrapers that feed on the abundant periphyton. In detritus-based streams, increased nutrients can lead to increases in microbial production on organic matter, which improves the quality of the food resource for shredder invertebrates. With higher food quality, macroinvertebrate production, particularly those taxa with short life cycles, can increase dramatically in nutrient-enriched streams.

Shifts in the invertebrate community associated with increased sedimentation have been observed in headwater reaches of agriculturally impacted streams. As the percent fine sediment increases, there is usually a shift from clinging and crawling taxa to burrowers. Insecticide runoff from agricultural fields into headwater streams can have more deleterious impacts on macroinvertebrate communities. Pesticides introduced into headwater streams can result in the loss of invertebrate species, cause shifts in functional production of invertebrates, and negatively impact ecosystem processes such as leaf litter breakdown and FPOM export.

Urbanization and Roads

Urban growth scenarios predict substantial increases in population and growth for many regions of the world. The replacement of forested land and riparian habitats with impervious surfaces such as roads,

Table 3 Examples of disturbances and their effects on benthic invertebrates in headwater streams

Disturbance	*Effect on invertebrates and stream function*	*Source*
Invasive species		
Gypsy moth defoliation	Accelerated detritus processing	27
Decline in eastern hemlock forests due to hemlock woolly adelgid	Reduction in alpha and gamma diversity of invertebrates and changes in trophic composition; pesticide inputs caused decline in invertebrate emergence; increased inputs of slow decaying wood; higher hydrologic variability	19, 20, 51
Loss of American chestnut trees as a result of chestnut blight	Decrease in leaf litter processing, quality of litter inputs, and invertebrate growth rates; increase in wood inputs and sediment stabilization	50, 57
Invasion of *G. pulex*	Increased predation on native invertebrates	28, 29
Agriculture		
Filling and tiling of streams	Reduced drainage density of stream network	59
Overapplication of fertilizer	Increased nitrogen alter food resources for invertebrates; increase in abundance, biomass and production of invertebrates; increased growth rates for short-lived invertebrates	13, 14, 16
Sediment runoff	Decline in Ephemeropteran, Plecopteran, and Trichopteran, and Coleopteran taxa; increases in chironomids, oligochaetes and molluscs	2, 6, 7, 24, 39, 44, 53
Insecticide runoff	Decline in invertebrate abundance, biomass, and production; loss of species; shifts in functional structure; decline in organic matter export and leaf breakdown rates	15, 31, 32, 33
Increased water temperature	Decline in Ephemeroptera, Plecoptera, and Trichoptera	24, 44
Urbanization and roads		
Altered hydrology and geomorphology, increased bacterial populations and turbidity, increases of pesticide, herbicide, and fertilizer runoff; decline in habitat	Decline in invertebrate diversity; decline in Ephemeroptera, Plecoptera, and Trichoptera; increase in number of pollution-tolerant taxa; decline in invertebrate production; decline in leaf breakdown rates	4, 9, 30, 39, 40, 48, 58, 60
Increased number of culverts	Reduced adult caddisfly diversity and abundance above culverts	5
Forestry practices		
Increased stream temperature, discharge, nutrients, and primary production; reduced organic matter inputs	Shift from allochthonous to autochthonous energy; increase in abundance, biomass, and production of taxa with short life cycles; leaf litter breakdown altered; significant reduction in invertebrate production with decline in detrital inputs	1, 3, 21, 23, 41, 42, 52, 55, 56
Sediment runoff from logging roads	Decline in total richness and abundance of all invertebrate taxa	22, 54
Mining		
Acid mine drainage and metal uptake	Reductions in abundances of sensitive invertebrate taxa; increase in tolerant taxa; decline in species diversity; increased drift; reduced community respiration; reduced secondary production	8, 11, 12, 18, 34, 45, 49
Mountaintop mining/Valley fill		
Burial of headwater streams; increased sedimentation, conductivity, and metals	Elimination of all biota in buried streams; downstream declines in Ephemeroptera richness, decline in abundances of Ephemeroptera, Odonata, Coleoptera; decline in scraper and shredder abundance	25, 43
Global climate change		
Channel drying	Altered organic matter standing crops, and invertebrate abundance and production; shifts from large-bodied, long-lived taxa to small-bodied, short-lived taxa	10, 17

Continued

Table 3 Continued

Disturbance	*Effect on invertebrates and stream function*	*Source*
Increased water temperature	Decline in total invertebrate densities, faster growth rates, reduced size at maturity, and altered sex ratios of some taxa	26
Wildfire		
Intense heating, altered water chemistry, food resources, hydrologic runoff patterns, vegetative cover, sediment transport	Shift in functional feeding groups that parallel changes in food resources; shift toward short-lived, trophic generalists; decline in invertebrate abundance and taxa richness	35, 36, 37, 38, 46, 47
Recreational activities		
Streamside camping, fishing, swimming, rafting, gold mining	Localized decline in abundance of scraper limnephilid caddisfly	61

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rooftops, and lawns alters the hydrology and geomorphology of streams. Increases in surface runoff associated with storm flow lead to declines in water quality, increases in bacterial populations and turbidity, and increases of pesticide, herbicide, and fertilizer runoff into nearby streams. Sediment runoff from construction sites and erosion due to downcutting result in habitat loss for aquatic life. Measurable aquatic degradation occurs with 6–10% impervious area and has been long been associated with decreased water quality of nearby streams. Urbanization in watersheds containing small streams usually results in less diverse invertebrate communities consisting of pollution-tolerant species. Culverts have been shown to act as barriers to upstream migration of adult caddisflies. Since many stressors associated with urbanization act synergistically, it is difficult to separate cause and effect of individual stressors on the invertebrate communities in small urban streams.

Forestry Practices

Logging results in changes in stream temperature regimes, increased discharge and altered hydrology, increased nutrient export and increased solar radiation and primary production, increased sediment export, and changes in dissolved organic matter derived from the terrestrial ecosystem. These changes are accompanied by substantial changes in the energy base of headwater streams, with a shift from allochthonous detritus to autochthonous production. The physical and energy base changes can lead to large changes in macroinvertebrate community structure. An experimental long-term reduction of organic matter inputs to a small stream in the southern Appalachians resulted in a significant decline in total invertebrate production. Invertebrate taxa with short life cycles and the ability to exploit increases in primary production greatly increase in abundance, biomass, and productivity. Studies in the central and southern Appalachians show that long-term patterns of leaf litter breakdown can be altered for many years following logging. However, depending upon the extent of terrestrial succession, invertebrate assemblages can revert back toward their prelogged condition.

Mining

Mining has severe consequences for benthic invertebrates in small streams worldwide. Effects of mining on macroinvertebrates in small streams are caused by acid mine drainage, sediments, or burial of the streams themselves. Acid mine drainage and the associated problems of heavy metal contamination usually results in reductions of numbers of sensitive taxa in the orders of Ephemeroptera (particularly those of the family Heptageniidae), Plecoptera, Trichoptera, Megaloptera, Odonata, and Diptera and an overall decline in species diversity. Some studies have shown that functional measures of benthic invertebrates such as drift and community respiration are also negatively affected by mining impacts. In recent years, the practice of mountaintop removal and valley fill mining has resulted in the filling and permanent burial of at least 1450 km of small streams in the Appalachian Mountains. The burial of multiple small streams destroys all aquatic life in these streams and results in declines of sensitive invertebrate taxa immediately below valley fills. The cumulative effects of burying multiple headwater streams on the water quality in downstream rivers should be evaluated.

Recreational Activities

Little information regarding the effects of recreational activities (e.g., horseback riding, cycling, all terrain vehicle use (ATV)) on small streams has been reported in the primary literature. One study suggested that populations of *Dicosmeocus gilvipes*, a scraping limnephilid caddisfly, in a fifth-order stream were affected by localized disturbances associated with multiple recreational activities such as gold mining, streamside camping, swimming, and fishing. With growing public demand for access to undeveloped land harboring networks of small streams for recreational activities such as off-highway vehicle use, there is an urgent need for more research examining the impacts of such use and ways to mitigate potential negative effects.

Global Climate Change

Consequences of global climate change on invertebrates in small streams will vary greatly spatially and temporally, thus making it difficult to predict potential effects. Generally, precipitation and evaporation are expected to become more variable over time. Some regions of the world will become wetter, while others will become drier, affecting runoff patterns. Increased temperatures as a result of global climate change will reduce snow cover and also affect hydrologic patterns in small streams. Shifts in hydrologic patterns (e.g., flooding, drying) will impact transport of nutrients, organic matter, and habitats available for colonization by benthic invertebrates. Changes in riparian vegetation may alter the quality and quantity of detrital inputs to headwater streams, thereby altering ecosystem processes (e.g., production, respiration, organic matter breakdown) within small stream reaches and longitudinally-linked downstream reaches, as well as invertebrate life histories and species composition. There is some evidence in the literature that the timing and duration of small stream channel drying results in altered organic matter standing crops, and invertebrate production. Furthermore, extended channel drying results in shifts from large-bodied, long-lived taxa to small-bodied, short-lived taxa. An experimental manipulation of thermal regime (2.5–3.0 °C increase in water temperature) in a small stream near Ontario, Canada, resulted in a reduction of total invertebrate densities, faster growth rates, reduced size at maturity, and altered sex ratios of some invertebrates.

Wildfire

Invertebrates in small streams are more susceptible to fire disturbance than those in larger streams. Intense heating, severely altered water chemistry, and the smothering of food resources by ash in smaller streams can kill invertebrates directly. Over longer time periods, changes in hydrologic runoff patterns, vegetative cover, channel morphology, and sediment transport also affect invertebrates in fire impacted streams. Changes in food resources over time result in changes in the functional characteristics of the macroinvertebrate community. Initially, scraper densities increase following a fire because of increased primary productivity associated with canopy opening and increased available nutrients. As transportable organic matter levels increase in the stream, abundances of collectors increase. Shredder populations are usually the last to recover since they depend on detrital inputs from the riparian habitat. Recovery of macroinvertebrate communities in intact, normally functioning small streams prior to fire usually occurs quickly (5–10 years) following fire disturbance and parallels the regeneration of the terrestrial vegetation. Short-lived invertebrate taxa that are trophic generalists, and have wide habitat preferences generally recover quicker.

Summary and Knowledge Gaps

The functional contributions of benthic invertebrates to small streams are well known. Hundreds of invertebrate species may be found in a small stream. Since headwater streams make up such a large proportion of total stream length in river networks, total invertebrate production in small stream segments may exceed that in large rivers. Invertebrates also represent an important link between terrestrial and aquatic ecosystems due to the close proximity of the two systems. A variety of environmental factors influence the types and productivity of invertebrates in small streams. Benthic invertebrates are also good indicators of the health of small streams. Human and natural disturbances alter typical macroinvertebrate assemblages in small streams which may have indirect effects on higher trophic levels and small stream processes.

In the last two decades scientists have begun to study macroinvertebrate communities and the ecological processes affected by invertebrates along longitudinal reaches spanning multiple stream orders. However, little information is known about the quantitative and qualitative contribution of headwater benthic fauna to the functioning of downstream ecosystems. In some cases, entire benthic invertebrate communities are being destroyed by burial or stream piping before the true diversity of organisms found in small streams is known. Furthermore, with an increasing number of disturbances that are large scale in magnitude, it is critical that scientists become better able to predict threshold levels of disturbance within headwaters of river networks such that downstream water quality and ecosystem functions are not irrevocably damaged.

See also: Acidification; Agriculture; Aquatic Insects – Ecology, Feeding, and Life History; Aquatic Insects, Classification; Aquatic Plants: A General Introduction; Aquatic Plants and Attached Algae; Benthic Invertebrate Fauna, Small Streams; Benthic Invertebrate Fauna; Bioassessment of Aquatic Ecosystems; Biodiversity of Aquatic Ecosystems; Biological Interactions in River Ecosystems; Climate and Rivers; Coarse Woody Debris in Lakes and Streams; Comparative Primary Production; Conservation of Aquatic Ecosystems; Decapoda; Deforestation and Nutrient Loading to Fresh Waters; Diptera (Biting Flies); Diptera (Non-Biting Flies); Ecology and Role of Headwater Streams; Effects of Recreation and Commercial Shipping; Ephemeroptera (Mayflies); Fires; Flatworms (Turbellarians); Floods; Fluvial Export; Gas Exchange at the Air-water Interface; Gastrotricha; Geomorphology of Streams and Rivers; Hemiptera (True Bugs); Hydrachnida (Water Mites); Invasive Species; Isopoda (Aquatic Sowbugs); Littoral Zone; Megaloptera (Alderflies, Dobsonflies); Mercury Pollution in Remote Freshwaters; Microbial Food Webs; Mollusca; Mosses (Bryophytes); Natural Organic Matter; Nematoda; Nematomorpha (Horsehair Worms); Neuston in Aquatic Ecosystems; Odonata (Dragonflies and Damselflies); Plecoptera (Stoneflies); Regulators of Biotic Processes in Stream and River Ecosystems; Restoration Ecology of Rivers; Restoration of Acidic Drainage; Riparian Zones; Streams; Subterranean Aquatic Ecosystems - Groundwater Ecology; Tardigrada (Water Bears); Trichoptera (Caddisflies); Trophic Dynamics in Aquatic Ecosystems; Urban Aquatic Ecosystems.

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